論 文 の 内 容 の 要 旨

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論文題目 Tracking data reveal seabirds' locomotion strategies in response to wind
(経路データから明らかにする海鳥の風に対する長距離移動戦略)

General introduction

Animal navigation has interested scientists for many decades, but is now seen as an emerging field owing to animal tracking technology. This technology has enabled the movements of numerous species to be recorded over larger spatiotemporal ranges at high resolution using GPS or satellite tracking. However the behavioral and cognitive mechanisms involved in long-distance animal orientation have yet to be resolved. To investigate the effects of external factors on navigational decisions by analyzing up-to-date, high-resolution animal trajectories requires a state-of-the art modeling approach. Wind is one of the important external factors that affect on birds' movement. By investigating birds' movement in response to wind, we can know their navigation strategy and capacity, but it has bee to measure the wind vector and the bird heading vector (birds velocity relative to wind) over the wide range where free-ranging bird travels.

In this thesis, a new statistical model is constructed. This model enables to estimate an external factor (ocean wind) and the animal's navigational decision-making (heading) simultaneously only from GPS tracking data. This model was applied to two seabird species, streaked shearwater (*Calonectris leucomelas*) and wandering albatross (*Diomedea exulans*). As these seabirds move over the ocean where landmarks are absent, it should be challenging for them to move toward distant goal by dealing with wind effect.

Seabirds' wind compensation over the sea

First, the statistical model to estimate the wind and bird's heading vectors form GPS tracking data was proposed. In previous models for animal directed movement toward a particular goal direction or location, it has been assumed that the track vector distributes symmetrically along its mean vector. However, in this thesis, it was shown that the heading vector is distributed "symmetrically" along its mean vector but the track vector should be distributed "asymmetrically" along its mean vector via the effect of the flow, and by utilizing the asymmetry the wind and heading vectors can be estimated from tracking data. The method was applied to the homing tracks of streaked shearwaters (*Calonectris leucomelas*) recorded at a resolution of one location per minute, and whether they were compensating crosswind was investigated. It was found that birds compensated side wind even though they were flying over the sea that indicating their high navigation ability. In more detail, the birds changed their orientation strategy during their homing. Intriguingly, the degree of compensation was higher when birds were flying over the sea near the coast than over open sea, indicating that in the former regions they might be able to see the coast and obtain the corresponding navigational cues that were not available when flying over the open sea. In addition, the preferred direction changed with respect to the regions. The intended goal direction of birds was accurately toward the colony (final goal) at the beginning of homing flights. However, as they approached the colony, their preferred direction deviated from the colony, indicating that they tried to reach the coastline which can be used as an additional navigational cue. Thus, although birds have a map sense and can compensate for wind over the open sea, they may also try to use landmarks depending on their availability.

Tail wind avoidance and zigzag homing of albatrosses

Wandering albatrosses (*Diomedea exulans*) are locomotor extreams that travel thousands of kilometers per foraging trip, searching for randomly distributed prey over the open sea. In this chapter, how the albatrosses go home when wind is blowing to their goal was investigated. First, the model introduced in chapter 2 was developed into state space model. This development enabled more robust estimation of time varying wind and heading vectors. The model was applied to tracks of wandering albatrosses. The estimated wind speed and direction showed good agreement with more temporally coarse wind data remotely sensed by satellite, Then, the bird moved directions relative to the wind direction were calculated at every minute. The results were that wandering albatrosses preferred crosswind. It was even the case when wind was blowing to their goal at their homing, and they avoided tailwind. This tailwind avoidance resulted in large-scale zigzag homing. This movement pattern of wandering albatross contrasts with that of flapping birds that prefer tailwind when wind is blowing to the goal, which is interpreted to exploit tailwind assistance.

To reveal the mechanical reason of the tail wind avoidance and zigzag homing of wandering albatross, numerical calculation was conducted. Wandering albatrosses is a specialist of wind- and wave-based flight—called dynamic soaring—to extract energy for highly efficient travel. First, one soaring cycle scale movement of dynamic soaring bird was investigated. Recent studies developed a framework to calculate the path and time series of body angles of dynamic soaring bird (or glider) that maximize interested value by applying an optimization calculation method to the physical model of soaring bird. Although the minimum wind speed required for sustainable dynamic soaring was particular interest of these studies, here, the upper limit of ground speed (averaged over one dynamic soaring cycle) a soaring bird can reach in a certain directions is calculated. As a result, how maximum speed changes depending on the bird moved direction relative to the wind direction was calculated. The birds ground speed reached maximum when bird fly with cross-tail wind and drastically decrease at more tailwind condition. Also, the results indicated there are two movement way to minimize the elapsed time to reach the goal located at leeward. One way is going to the leeward goal straightly (Beeline strategy), and the other way is move to the leeward goal by showing large-scale zigzag movement. Then, additional numerical simulation was conducted for investigating large-scale optimum path planning of dynamic soaring birds. It was found that the zigzag homing outperforms the beeline homing under the conditions wind direction fluctuates. In reality, wind fluctuate should exist to some extent, and hence birds might have preferred zigzag homing and avoided tailwind even though the wind was blowing to the goal. Overall, our results indicate that albatrosses determine their movement direction based on their maximum ground speed in which the more he/she moves to leeward, and the zigzag homing was an optimal movement way for albatrosses.

General discussion

In the first part of this thesis, the ability and sensors required for movement strategies reported in the previous chapters, the wind compensation over the sea and the large-scale zigzag homing by avoiding tailwind, were discussed. It was concluded that at least three abilities are required - (i) the ability to find their location in the environment where landmarks are poor (map sense), (ⅱ) ability to detect wind direction and speed, and (ⅲ) ability to control their flight to move toward intended direction based on their location and wind. Although the results cannot identify the mechanism that enables these abilities, magnetic and olfactory senses can be possible mechanisms and cues that realize those abilities. In the later part of this thesis, the statistical approach to inversely estimate unobservable causal factors from observed output data, called invers problem approach, was explained. Although this approach has been common in physics and engineering, it is still not common in animal ecology. To apply inverse problem approach to animal behavior, the different point of animals compared to lifeless things were be noted. Especially, although animal movement is inevitably constrained to physical rules, they can dynamically adjust their behavior and property in adaptive way. To deal with this problem state space model is explained as a promising framework for combining inverse problem approach with bio-logging data and that enables to estimate the variables that seem impossible to measure and enables to test hypothesis that seem difficult to test in the field.